Variation and Relative "Niche" Size in the Sea Mussel *Mytilus edulis* in Association with *Mytilus californianus*

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INTRODUCTION

Mytilus edulis (Linnaeus, 1758) IS WIDESPREAD in both northern and southern hemispheres (STUBBINGS, 1954). SEED (1969) describes distribution in the northern hemisphere as almost cosmopolitan. Variability in shell morphology of this animal has been the subject of many reports in taxonomic literature. For instance, one variant, *M. galloprovincialis* (Lamarck, 1819), synonymized by SOOT-RYEN, 1955, has been the object of considerable conjecture as to its morphological variation and degree of overlap with *M. edulis* (HEPPER, 1957; LEWIS & SEED, 1969). LAMY (1936) lists no fewer than 16 different synonyms for *M. galloprovincialis* (then considered a full species). At present, it is problematical as to whether such variation occurs as the result of developmental plasticity, different forms being ecological variants (STUBBINGS, 1954), or whether they should be looked upon as distinct genetic types, perhaps subspecies. LEWIS & SEED (*op. cit.*), after an extensive investigation of variability in *M. edulis* from S. W. England, concluded that two distinct forms inhabited the area; however, variable morphological characters in both forms resulted in overlap, making distinction difficult. The forms in question were the "Padstow type" (cf. *M. galloprovincialis*) and *M. edulis*; both were living together in most locations.

In a study of factors influencing shell shape in *Mytilus edulis*, utilizing transplantation experiments, SEED (1968) indicated environmental differences contributed greatly to modifications of form in the species. Young mussels from different locations appeared similar to each other, but with increasing size animals progressively differed in height (dorsal to ventral) with respect to length (anterior to posterior) of shells. Smaller mussels from all habitats investigated showed striking uniformity in gross shell morphology.

This paper reports further investigation into factors affecting morphological variation in *Mytilus edulis*.

MATERIALS AND METHODS

During an investigation of the biology of *Mytilus edulis* I looked at several hundred animals from the east coast of North Amcrica taken from both sheltered (bay) and cxposed environments near Cape Ann, Massachusetts, as well as west coast populations from Southern California (San Diego to Monterey), involving many thousands of individuals.

Mussels from locations used in experiments reported here were gathered and transported to Santa Barbara (California) within a period of one day for west coast samples and two to three days for those from the east coast: the latter samples were transported in refrigerated Dewar Flasks.

Once in the laboratory, east coast mussels were placed in refrigerated circulating sea water at a temperature of 9° C. During the subsequent week temperature was increased slowly to that of the local sea (19° C). Throughout this period mortality of east coast mussels did not differ significantly from that of a group of Santa Barbara mussels held in the laboratory for the same length of time. At the end of this period east coast mussels werc transferred to experimental cages.

Experimental populations were placed in cylindrical wire mesh cages measuring 8.5 inches (21.5 cm) in height and 7 inches (17.78 cm) in diameter, constructed from galvanized hardware cloth sections of $\frac{1}{4}$ or $\frac{1}{2}$ inch (0.63 or 1.27 cm) mesh which were coated with epoxy resin to stabilize the binding and reduce zinc corrosion. These cages were suspended from the end of the Signal Oil and Gas Company's pier at Ellwood (a large steel structure extending almost half a mile from a sandy shore into open sea, located 14 miles west of Santa Barbara).

Differences between *Mytilus edulis* from the East and West Coasts of the U. S. A.

As a group, east coast mussels tend to have narrower shells than those from the west coast (the width of a shell being defined as the maximum distance from the dorsal

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to the ventral shell margin), but this can be masked by development under different environmental conditions. For example, east coast (Massachusetts) samples from a sheltered bay and an open shore, together with west coast samples from a moderately sheltered region (Ellwood Pier) and an exposed region (Point Mugu, California), showed no overall difference in shell width between populations from the two coasts (Table 1). However, in this example a significant difference in shape was detected between mussels from exposed regions and those from sheltered regions, indicating that animals from exposed regions have narrower shells than mussels from sheltered regions.

In an attempt to determine the effect of geographical origin on shell width, without the complication of differing physical environments, a group of small east coast mussels (less than 1 cm long), taken from both exposed and sheltered environments, were placed in a cage suspended 2 feet below extreme low water level at Ellwood Pier for a period of 1 month (26 December 1966 to 26 January 1967). Mortality during this time was approximately 50% (see later). Subsequently, these animals were compared with a control population of west coast mussels (from Ellwood Pier).

West coast mussels were significantly wider than those from the east coast (Table 2). It would seem, therefore, that a definite difference in shape (presumably genetically determined) exists between these samples from the east and west coasts, which can be masked by the effects of differing physical environments. Small, newly-set mussels from sheltered and exposed environments on the west coast exhibit no obvious morphological differences.

Mytilus edulis taken from sheltered environments (harbors) between San Diego in the south and Monterey Harbor in the north showed no significant differences in shell width with respect to shell length.

Growth rates of 2 groups of mussels from the east and west coasts were also studied at Ellwood Pier. Each of 45 mussels from the east coast, ranging in size from 1.5 cm to 6.5 cm in length was marked and matched according to size with a corresponding mussel from the west coast. Both groups were then placed in separate cages below low water level at Ellwood Pier. After one month (26 December 1966 to 26 January 1967) analysis showed that

Table 1

Comparison of shell widths of *Mytilus edulis* populations collected from the mid-tide level on the East and West Coasts of North America and from both sheltered and exposed positions (see text). The dependent variable is shell width and the independent variable is shell length. (All measurements are in centimeters)

Note: In this and the other tables used in this report, one asterisk (*) indicates significance at the 5% level, two asterisks (**) significance at the 1% level, and three asterisks (***) significance at the 0.1% level. Abbreviations of statistical terms are those used by J. C. R. LI (1964).

Group	Sample Size	Regression Equation	Slopes F 3,132	Adjusted Means at x = 2.79	F 3,132
1. East Coast Mussels (Protected)	39	y = 0.04+0.51x	0.75 NS	1.51	2.38 NS
2. East Coast Mussels (Exposed)	17	y = -0.08+0.55x		1.45	
3. West Coast Mussels (Protected)	54	y = 0.25+0.47x		1.56	
4. West Coast Mussels (Exposed)	26	y = 0.15+0.48x		1.47	

Individual D. F. Tests on Adjusted Means

	F
1.3/2.4	3.36*
1.2/3.4	2.83 NS

Table 2

Comparison between the mean shell widths of *Mytilus edulis* populations from the East and West Coasts of North America after growth in cages at Ellwood Pier, California. The dependent variable is shell width and the independent variable is shell length.
(All measurements are in centimeters)

Group	Sample Size	Regression Equation	Slopes F 1,65	Adjusted Means at x = 2.2	F 1,65
1. *Mytilus edulis* from East Coast	33	y = 0.01+0.56x	8.17**	1.23	12.60**
2. *Mytilus edulis* from West Coast	34	y = 0.72+0.30x		1.38	

the west coast mussels exhibited the greatest growth ($p < 0.05$). (During this time the east coast mussels suffered a mortality of 50% and the west coast mussels a mortality of 12%.)

The previously mentioned group of small east coast mussels grown in a cage at Ellwood Pier was initially comprised of 60 individuals; after one month, however, only 33 remained. During this time growth resulted in change of mean size of 1.00 cm to 2.08 cm. This is not significantly different from the highest growth rate recorded for west coast mussels at Ellwood Pier (HARGER, 1970b). An apparent conflict exists between the growth results obtained from this experiment and those reported for the "matched" experiment where west coast mussels grew faster. A possible explanation is that many of the east coast mussels used in the latter experiment had attained maturity on the east coast shore, whereas the small mussels developed on the west coast (suffering 50% mortality in the process), and survivors were presumably selected by local conditions. Although there are distinguishable differences between these populations from east and west coast, a considerable degree of overlap exists in their morphological (shape) and physiological (growth rate) properties.

Mytilus californianus Conrad, 1837, appears to be endemic to the west coast of North America and has a range extending from the Aleutian Islands to Isla Socorro, Mexico (SOOT-RYEN, 1955). It is confined principally to regions of open coast but may penetrate into quieter waters where *M. edulis* is predominant (SHELFORD *et al*, 1935; HARGER, 1970b). Specimens of *M. californianus* taken from the mid-tide level in areas exposed to heavy wave shock (Cayucos Pier and Monterey Peninsula) are slightly narrower than specimens taken from quieter regions (Ellwood Pier and Stearns Wharf) (Table 3). Relative wave impact indices for the 4 locations referred to above are: Monterey Peninsula, 1.00; Cayucos Pier, 0.27; Ellwood Pier, 0.16; and Stearns Wharf, 0.016 (HARGER, 1970a). This relationship (between shell width and wave impact) is difficult to demonstrate unless differences in wave impact are extreme. For instance, mussels at Ellwood Pier are not significantly narrower than those at Stearns Wharf (Table 3).

Mytilus edulis exhibits distinct variation correlated with differences in wave impact (Table 1). Also, SEED (1968)' and LEWIS & SEED (1969). Both dry body weight and upper size limit vary with relative wave impact (HARGER, 1970a). Such relationships tend not to occur in *M. californianus* (HARGER, 1970a). Growth of *M. edulis* is adversely affected by wave impact, whereas that of *M. californianus* is not (HARGER, 1970a).

Mussels taken from a clump 7 feet in diameter at Ellwood Pier, containing both species, showed the following characteristics. For both *Mytilus edulis* and *M. californianus* there was no significant difference in width with respect to length between samples from inside and outside of the clump or between the top, middle and bottom positions (for terminology referring to clump structure see HARGER, 1969). A sample of *M. edulis* obtained from the mid-tide level at Stearns Wharf, however, yielded mussels on the inside with narrower shells than those on the outside ($P < 0.05$). When depth (maximum distance between the outside surfaces of the 2 valves) with respect to length was investigated for *M. edulis*, no difference was apparent between samples from top, middle and bottom clump positions; however, those from the inside samples, as a group, were deeper than those from the outside ($P < 0.001$). In the case of *M. californianus*, no significant differences among the samples from top, middle and bottom positions, inside or outside, could be detected.

Table 3

Comparison among the mean shell widths of *Mytilus californianus* populations collected from the mid-tide level in areas exposed to extremely heavy wave impact (Cayucos Beach and Monterey Peninsula) and from sheltered areas (Ellwood Pier and Stearns Wharf). See HARGER (1970a) for details of exposure estimations. The dependent variable is shell width and the independent variable is shell length. There is no significant difference between treatments 1 and 2 or between 3 and 4 in slope of regression or y adjusted values.
(All measurements are in centimeters)

Group	Sample Size	Regression Equation	Slopes $F_{3,199}$	Adjusted Means at x = 5.29	$F_{3,199}$
1. *Mytilus californianus* from Ellwood Pier	46	y = 0.40+0.43x	9.41***	2.68	54.57***
2. *Mytilus californianus* from Stearns Wharf	52	y = 0.70+0.39x		2.76	
3. *Mytilus californianus* from Cayucos Beach	46	y = 0.48+0.37x		2.44	
4. *Mytilus californianus* from Monterey Peninsula	53	y = 0.38+0.37x		2.35	

	$F_{1,199}$
Individual D. F. Test on B	
1.2/3.4	18.28***
Individual D. F. Tests on Adjusted Means	
1.2/3.4	152.06***

In both *Mytilus edulis* and *M. californianus* an increase in exposure to wave impact is correlated with an increase in shell weight. In the case of *M. edulis,* the relationship is probably complicated by the presence of *M. californianus* as a consequence of competitive interaction. Individuals of *M. edulis* from pilings in Santa Barbara Harbor and those from Ellwood Pier have lighter shells than those from the more exposed Goleta Point shore ($P < 0.001$). *Mytilus californianus* from mid-tide level in extremely exposed locations, such as Cayucos Beach, tend to have heavier shells than individuals growing in clumps on adjacent pier pilings ($P < 0.001$). There is, however, no significant difference in shell weight between mid-tide populations growing on Ellwood Pier, on Ellwood shore, on Stearns Wharf, or on the Pier at Cayucos. Thus, *M. californianus* shell weight seems to be uniform over a wide range of environmental conditions. The problem with relying on such data to evaluate variability is that it is not possible to be sure that animals have been exposed to various environmental factors acting at each location for the same time period. This problem can only be eliminated by performing transplantation experiments.

TAXONOMIC VARIATIONS

The extensive lists of synonyms for *Mytilus edulis* given by LAMY (1936) and SOOT-RYEN (1955), together accounting for a total of 57 different forms from all over the world, suggest this species is extremely variable, or at least exhibits sufficient variability to yield a number of forms which have been accorded specific, subspecific, and even varietal status during recent time.

These synonyms could simply be due to careless taxonomy and may have little to do with variability as such. However, of all the species in the family Mytilidae listed by SOOT-RYEN (1955) *Mytilus edulis* has 25 synonyms, whilst the 3 species with the greatest number after *M. edulis* have 8, 5, and 4 synonyms, respectively. Of the remaining 52 species, nearly half have no synonyms. A similar relationship can be found within the Mytilidae reviewed by LAMY (1936).

It would, of course, be preferable to base an estimate of variability on "races" or recognized forms, and in this context Soot-Ryen (1955) lists 7 subspecific units for *Mytilus edulis* and one for *M. californianus*. In contrast to *M. edulis*, *M. californianus* has only one synonym, and that is probably due to a misinterpretation.

DISCUSSION

Why should *Mytilus edulis* be extremely variable in form and *M. californianus* be conservative? In the first place, one might expect widely separated populations to evolve in response to local conditions, so that populations of *M. edulis* in New Zealand would be different from those in North America. Lamy (1936) lists a total of 37 synonyms, originating chiefly from European coasts, for *M. edulis*. This in itself might suggest that *M. edulis* is an exceptionally variable animal – even within one geographical area. Five new synonyms only have been used for *M. edulis* on the coasts of North America, possibly indicating more restricted variation among North American populations. This limited number of synonyms may perhaps be accounted for in the following ways:

(1) Early taxonomists working with new world shells possessed a large repertoire of "European" names which they subsequently applied to North American forms.

(2) The high number of forms initially proposed by European workers is related to the large numbers of amateur naturalists who were working in that area; a number which was, in all likelihood, much higher than in North America.

(3) Possibly restrictions are imposed upon the range of *Mytilus edulis* through competitive interactions with *M. californianus* in open coast situations on the west coast of North America, reducing the potential variability of the former species.

In the British Isles *Mytilus edulis* occurs both in sheltered regions and on exposed coasts (Kitching *et al.*, 1959, Lewis & Seed, 1969). Lewis & Seed (*op. cit.*) report this species as occurring on "slightly less than extremely exposed coasts" and present in the form of "small closely packed seed mussels, not as the large individuals found on shingle and mud in the straits." In the same paper they further comment on the marked dissimilarity of the 2 habitats in which *M. edulis* is found, namely on clean exposed rocks or on low level stone and mud shores in sheltered and sometimes brackish waters. Seed (*op. cit.*) comments to the effect that high densities of small *M. edulis* on exposed coastlines must constitute the majority of mussels in British waters.

I have shown (Harger, 1967) that growth of *Mytilus edulis* on the coast of Southern California may be limited by competitive interaction with *M. californianus*. The outer coast habitat is not here as readily available to *M. edulis* as is similar exposed coast around Europe. If competition with *M. californianus* has restricted variation in form of west coast *M. edulis* populations, then as a result it can be expected that both European and east coast North American populations will show greater variability than those inhabiting the west coast of North America. In both Europe and east coast North America, *M. edulis* is the only species in the genus present on rocky intertidal shores.

Variation among European populations is considerable, as noted by Lewis & Seed (1969) and Seed (1968); however, the task of rating variability in east and west coast North American populations is difficult.

There have been 2 forms of *Mytilus edulis* described as new species from the west coast; these are *M. glomeratus* Gould, 1851 and *M. trossulus* Gould, 1850. In addition, one form from Southern California was accorded subspecic rank – *M. edulis diegensis* Coe, 1945. (See also Coe, 1946, for a full account of this form.) These have all been synonymized by Soot-Ryen, 1955, on the basis of intergrading shell characters. In addition, when typical open coast forms of *M. edulis* (forms characterized by narrow shells and a generally gnarled and stubby appearance, *i. e.*, *M. glomeratus*) were allowed to develop in cages suspended in the Santa Barbara Harbor, the final shape was found to be similar to that of mussels which had spent all their lives in the harbor. An initial rough portion of shell remained on the transposed mussels, although new growth was normal and relatively smooth (see also Seed, 1968). On the east coast 2 forms have been described as new species; these are *M. notatus* (DeKay, 1843) and *M. minganensis* (Mighels, 1844). One cannot reject the hypothesis of there being no difference in variability between east and west coast populations on the basis of the new forms described in both areas, since among the total number of different synonyms used for populations of the two coast lines (including native European names) perhaps 7 or 8 different names have been applied to west coast populations (Soot-Ryen, *op. cit.*), a minimum of 8 or a maximum of perhaps 13 have been used for east coast forms (Binney, 1863). (I am unable to obtain an accurate count of the different synonyms used for east coast forms, since an adequate taxonomic revision of east coast Mytilidae has not yet been undertaken.)

Seed (1968) considers that because *Mytilus edulis* possesses a planktonic phase in its life history, allowing colonization of widely differing habitats, a genotype capable of wide phenotypic expression would be of great survival value. Since the larvae remain in the plankton for a considerable time, during which they are carried some distance, it would seem most improbable that natural selection could act in such a way as to produce a shell form suited to a particular set of environmental conditions. SEED (*op. cit.*) contrasts this state of affairs with that for *Thais lapillus* (Linnaeus, 1758) (in the Santa Barbara region *T. emarginata* (Deshayes, 1839) would be the ecological equivalent), where egg capsules are laid and the young develop in the same locality as their parents, enabling natural selection to produce genotypes most suited to the environments in which they live. This results in locally distinct populations differing considerably in genetic makeup (STAIGER, 1957). Both *Mytilus edulis* and *M. californianus* appear to reproduce by means of the same mechanism, and consequently their differing population characteristics must be due to selective survival in differing locations.

In this connection, it can be noted that *Mytilus edulis* denies *M. californianus* access to quiet waters. This is accomplished by a difference in crawling behavior whereby *M. edulis* is able to arrange itself on the outermost surfaces of mixed species clumps, resulting in enclosed mussels being smothered by silt (HARGER, 1968, 1970b). This behavior effectively confines *M. californianus* to regions where water movement is sufficient to largely prevent accumulation of particulate matter in mussel clumps, *i. e.,* the region of the open coast. The great morphological plasticity of *M. edulis,* however, allows it to penetrate into such habitats.

As stated previously, east coast mussels are narrower than those from the west coast, also mussels growing in exposed areas tend to have narrower shells than those in sheltered areas (Table 1). I have shown (Harger 1970a) that the force required to remove west coast *Mytilus edulis* from their attachment points is not related to shell area in a simple linear fashion, as is the case for *M. californianus.* Specimens of *M. edulis* up to a length of 3 - 4 cm are removed by a force which is proportional to their shell area; however, larger animals are removed by the force normally required to remove an individual 4 cm in length.

It would seem that those animals having narrow shells would be at a selective advantage in open coast situations, since, length for length, the average shell area of such animals is less than that of wider forms. Consequently, mussels with narrow shells would be less likely to be washed away by waves. This, in turn, possibly indicates that selective forces may have permitted a relatively narrow-shelled population to evolve on the east coast, a population in part adapted to living on open coasts as well as in quiet bays. I assume that development of a form with a narrow shell on the south west coast of North America is prevented by competitive interactions with *Mytilus californianus* by a combination of 2 mechanisms: first, through direct competitive elimination, and second, by the fact that the presence of *M. californianus* seems always to enhance survival of *M. edulis* in the face of wave action by affording the latter some protection (HARGER, 1970c). Continual interchange between populations growing in sheltered harbors and those on the open coast also probably tends to override specific development of narrow-shelled forms in this location.

It is difficult to determine whether the presence of *Mytilus californianus* on the west coast has resulted in a reduction in "niche size" for *M. edulis* in this region. On the one hand, the presence of *M. californianus* serves to deny *M. edulis* a portion of the environment which would otherwise be open; on the other hand, however, *M. californianus* populations provide a certain amount of protection to *M. edulis,* enabling the latter to maintain substantial populations in areas experiencing moderate to heavy wave exposure (HARGER, 1970c) without necessitating development of obvious structural modifications.

The findings of LEVINS (1968) indicate an expectation of broad-niched species being associated with environmental variability (either in time or space or both). Certainly SEED (1969) places a high priority on such environmental variability as serving to cause extreme morphological variability in European populations. By the standards of its world-wide distribution, *Mytilus edulis* should be accorded the classification of possessing a broad niche, if variability of form is a reflection of such status; then, reduction of variability should indicate niche restriction. In all, taking into account experience with *M. edulis* from both sheltered and exposed shores in California, this animal here appears to be much less variable than populations described from Europe; perhaps this is due to competitive restriction by *M. californianus.* If such is the case, *M. edulis* populations from the east coast of North America should show greater variability of form than those from the west coast. The question concerning the cause of the comparative restricted variability of form in *M. californianus* must remain largely unanswered, except to point out that it is associated with comparative geographical restriction (compared with *M. edulis*); which in turn suggests a dependent relationship between phenotypic expression and relative efficiency at exploiting the open coast habitat.

CONCLUSION

I have suggested that variations in shell shape between populations of *Mytilus edulis* from the east and west coasts of North America may be due to a basic genetic difference. Variation within both populations (caused by local environmental conditions) can mask this.

I have further suggested that an apparent low variation in form shown by west coast North American populations (when compared to that of European populations) might be due to the effects of competitive interaction with *Mytilus californianus.*

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CORRECTION

On October 4, 1971, the author advised us that he discovered an error in his paper "The effect of species composition on the survival of mixed populations of the sea mussels, *Mytilus californianus* and *Mytilus edulis,*" which appeared in The Veliger 13 (2): 147 - 152. The following corrections are to be made:

p. 148, first column, line 16, should read

large (8 - 10 cm), medium (5 - 6 cm), and small (3 - 4 cm)

p. 148, second column, line 12 after Table 1, should read

of large mussels (8 - 9 cm). As far as possible, the mass